Diet and Feeding in the Freshwater Crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney Region, Australia

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Detailed analyses of gut contents, and field observations of feeding behaviour, clearly indicate that *Euastacus spinifer* is an opportunistic omnivore; diet does not vary with size, age or sex and much of the food is terrestrial in origin. The bulk of the diet comprises partly decomposed woody materials, but decomposing angiosperm macrophytic material is also consumed with occasional diatoms; small aquatic animal prey are actively hunted at times. It is suggested that nutrients are largely derived from fine organic particles associated with detritus, with supplements from scavenging and predation.

The common browsing feeding pattern is not planned or premeditated. A variety of materials can be cropped or gathered in different ways and food particles of widely disparate size are manipulated. The periodic hunting is a premeditated activity involving deliberate stalking of mobile prey and rapid ambush. The occasional bulldozing mode may be a response to scarcity of food but details of preferred food particle size and contributions of specific sources remain unknown.

Preliminary trials demonstrate that both hepatopancreatic fat content and protein concentrations in gastric fluid show wide individual variation, suggesting fluctuating feeding success. Future trials, to test for an index of nutritional state, should be of short duration, with larger samples at a single moult stage. Factors suggested as contributing to variation in feeding success among wild populations include seasonal changes and food availability.

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INTRODUCTION

Crustacean nutrition is generally poorly known with most research based on marine prawns or lobsters (Goddard 1988). Studies of crayfish diets and feeding behaviour, both in Australia and elsewhere, have largely focussed on species with commercial potential (Merrick and Lambert 1991). Although qualitative information on natural foods of these cultured species has often been available for some years, detailed quantitative dietary analyses and investigations of nutritional requirements are more recent (O'Brien 1995). Some data are available for several Australian parastacids with no commercial importance, for example, two *Engaeus* species (Suter and Richardson 1977) and *Parastacoides tasmanicus* (Lake and Newcombe 1975). But only a few general comments have been published about the natural diets of *Euastacus* species (Merrick 1993).

Natural Diet, Feeding Behaviour

The unusual polytrophic role of crayfishes in aquatic systems has now been acknowledged (Goddard 1988; Hogger 1988), but a few general findings have emerged

from studies to date and these are listed below. Firstly, their diet consists largely of plant debris, although the prime nutrient source is considered to be micro-organisms and fungi epiphytic on the detritus (Hogger 1988). Secondly, in order to utilise a wide variety of foods, crays possess a complex digestive system (Holdich and Reeve 1988). Thirdly, crayfish biomass is high when compared with other consumers which cannot utilise detritus or living vegetation (Hogger 1988). Fourthly, although other aquatic invertebrates are commonly cited as prey items, cannibalism is also an important aspect of feeding activity (Goddard 1988). Finally, juveniles generally feed more extensively on aquatic invertebrates and show more definite preferences for sizes or species of live foods (Goddard 1988; Warner and Green 1995; Warner et al. 1995).

Nutritional State

Although data on nutritional requirements of crays are still scarce (Goddard 1988) several general points are relevant here. Studies on omnivorous species indicate that good growth is only achieved when dietary protein exceeds 20% (Tsvetnenko et al. 1995) and that food consumption can be high (12–26% body weight/day) in juveniles, declining in adults to 2–3% body weight/day (Musgrove, 1993; Warner and Green 1995). Finally, the seasonal changes detected in lipid, carbohydrate and protein levels of tissues have, for one species, been associated with lowered lipid reserves at the end of the reproductive period (Fernandes et al. 1995).

Growth rates of individuals of *Euastacus spinifer* in the wild population are very variable (Turvey and Merrick 1997a,c). When considered in conjunction with the very patchy distribution of plant debris on the stream bed, the hypothesis was formulated that variation in growth might have related to variable feeding success; however, to investigate feeding success some form of index or measure of nutritional state is required.

In other studies previously reported *E. spinifer* could only be captured in numbers by using baits and this involves interruption of the normal feeding pattern (Turvey and Merrick 1997b). The volume of stomach contents of such animals could not be used as a measure of feeding success and the need for some estimate of average feeding success over a longer period was indicated. Studies of various decapods found that amounts of food consumed over a period affected both the dry weight and fat content of the hepatopancreas (Armitage et al. 1972; Heath and Barnes 1970; Stewart et al. 1967). Dall (1974) also found that hepatopancreatic solids of the spiny lobster *Panulirus longipes* decreased during starvation, but in addition, found that the protein concentration in gastric fluid decreased with decreased feeding, and was a reliable indicator of nutritional state (Dall 1975).

The objectives of the studies reported here are: to document in detail the major components of the diet; to investigate possible relationships between amounts of food consumed over time with fat content of the hepatopancreas and protein concentrations in gastric fluid: to discuss environmental factors that may influence feeding success.

MATERIALS AND METHODS

Natural Diet

For examination of gut contents individuals were fixed in 10% formalin immediately on capture. Samples were collected from several pools at the Loddon River study site (lat. 34°17′S: long. 150°54′E) south of Sydney (Turvey and Merrick 1997a) on three separate occasions (May, June, December) over a 30 month period.

Individuals were separated into four carapace length (CL) classes (20–30 mm,

30–40 mm, 40–50 mm, and 50+ mm). Cardiac stomach contents were removed from each cray and combined for animals in each size class. Each combined sample was separated into two particle-size fractions, by sieving through 0.5 mm mesh, to facilitate examination of constituents. Coarse material was observed using a dissecting microscope while finer material was examined under higher magnification, and the constituents were described qualitatively. With samples taken later in the study the contents of hindguts of five individuals were treated in the same way as stomach contents. Maximum dimensions of some of the smaller particles from both stomach and hindgut were measured using a graduated microscope eyepiece. Results of these analyses were compared with the observed feeding behaviour of captive *E. spinifer* and other species of *Euastacus*.

Feeding Trials

Two feeding trials were conducted and details of both experiments (including design, feeding regimes) are listed in Table 1. In the first trial, crays were allocated so that there were no significant differences between either means or variances of weights of individuals in each feeding group. During acclimation (to aquarium conditions and maintenance routine), the amount of food consumed (by each individual) at each feeding was determined. At the end of the trial the hepatopancreas and carcass (including all fluids released during dissection) were oven dried at 105°C for 24 hours. Moult increments during the experiment were compared with increments in wild crays. Moult increments, in Loddon River populations, were determined by comparing the difference in CL values over a known interval with annual frequencies calculated from the size class (Turvey and Merrick 1997b). Experimental individuals were paired with wild individuals of the same sex and similar carapace length, and the mean of differences between moult increments in each pair was tested for significance using a paired t-test.

TABLE 1

A summary of stocks, treatments and durations of *Euastacus spinifer* feeding trials.

Experiment	Stock (*) Size	Acclimation Period	Experimental Period (▲)
Trial 1	6 ♀(immature)	12 weeks	12 weeks
	+ 6 ♂	Fed 3–4 times per week (†)	Group a — fed every 3 days
	(20–240g)		Group b — fed every 9 days
Trial 2	9 ♀(immature)	2 Weeks	8 weeks
	+ 9 ♂	Fed 5 times per week (▼)	Group a — fed every day or two
	(20–30 mm CL)		Group b — fed every 7 days

* Each experimental individual allocated randomly to glass aquarium (45 l capacity); aquarium aerated, bottom covered with sand from study site, plastic flower pot provided for shelter; all aquaria subject to ambient temperatures and photoperiod.

† During this period all individuals fed with fish pieces, prawns or specially prepared pelletised food (Balazs et al. 1973).

▲ All tanks containing experimental individuals were cleaned and uneaten food removed the morning after each feeding; amount of food consumed calculated as difference between weight of food introduced and weight (adjusted for water uptake) removed.

▼ All individuals fed with earthworms and leaf litter in the evening.

In the second trial, experimental crays were allocated randomly to two feeding groups after acclimation. All individuals were fed on the last night of the experiment, then starved for three days until most of the ingested material had been eliminated from the digestive tract. All the animals were immobilised by immersion in an ice-water slush (30 minutes) and 0.05 - 0.1 ml of gastric fluid was then collected by applying gentle suction to a glass cannula inserted into the cardiac stomach (Vonk 1960). Each gastric sample was centrifuged (3,000 rpm for 2 minutes) and then two sub-samples of supernatant (0.01 ml each) were collected using 'Microcap' micropipettes; each sub-sample was diluted in 0.99 ml of distilled water.

The protein concentration in each 1% solution of gastric fluid was determined spectrophotometrically using the Biuret method (Layne 1957). Mean protein concentrations were calculated for all individuals, and 95% confidence limits for these means were determined using the 'samples' mean square in the analysis of variance (Snedecor and Cochran 1967). Percentages of total variability in protein concentration due to differences between feeding levels, crayfishes within feeding levels, and samples for each crayfish were calculated using the methods of Winer (1971). Moult stages were rated according to the modified universal moult stage notation (Passano 1960); the stages (and rating features) reported in these feeding studies are listed in Table 2.

TABLE 2

Moult stage notations and criteria used in rating experimental individuals and outgroup comparative field samples (based on Passano (1960)).

Notation	Position in Moult Cycle	Physical Characteristics
Ce	Early inter-moult	Branchiostegites deformable under light pressure, no gastroliths, absence of reddish-brown deposits on ventral surface.
C	Intermoult	Exoskeleton firm all over, no gastroliths, slight to heavy deposits on ventral surface.
De	Early pre-moult	Exoskeleton firm all over, gastroliths present, new exoskeleton not obvious, or slight.
Dl	Pre-moult	Branchiostegites deformable under light pressure, large gastroliths, new exoskeleton obvious and well-formed.

Protein concentrations of gastric fluid were also measured from a sample of wild crays captured at the study site shortly after the end of the trial and these values were compared with those of experimental individuals. The wild crays were starved for three days before gastric fluid samples were taken.

Hepatopancreatic fat determinations of experimental crays were based on small samples of hepatopancreas taken at the termination of the trial. This material had been fixed and stored in Bouin's fixative (Humason 1972). Samples were soaked in water for 48 hours and vacuum-dried to constant weight. Fat content was measured as the decrease in dry weight of the samples after refluxing with diethyl ether in a Quickfit 'Soxhlet' extraction apparatus for 16 hours. This fat was expressed as grams per gram of the initial dry weight of each sample and the difference in mean fat content between groups fed at two rates was tested for significance using a t-test. Using identical methods hepatopancreatic fat content was also determined for 13 wild crays (moult stages Ce and De) collected from the study site in August and January. Moult increments of experimental and wild individuals, of a similar CL, were compared as for Trial 1.

RESULTS

Natural Diet

Stomach contents comprised a mixture of particle sizes up to a maximum of 5mm. The largest size grouping (1–5mm) was recognisable as wood, bark and twigs, with occasional severely decomposed fibrous pieces of ribbon weed leaf (*Triglochin procera*). The woody fragments were either weathered, discrete particles, or had been torn, chewed or broken from some larger object. These particles were typically blackened and in a state of partial decomposition.

Most particles were less than 0.5mm (maximum dimensions) and ranged down to 2–10 μm, although small quantities of much finer material were also present. In all samples, a small proportion of particles down to 5 μm were identifiable as elements of woody plant tissue. Apart from very occasional diatoms, no algal material was obvious and, except for a few small sand grains (maximum dimensions of 0.1mm), the remainder of the fine material was unidentifiable.

Hindgut contents were identical to stomach contents except that the largest particles were only 1.0mm; most particles corresponded to the common small category in the stomach (2–10 μm). There was no obvious variation in gut contents with respect to either size of the individual or season.

Feeding Behaviour

The behavioural patterns considered to be associated with feeding have been divided into three categories: browsing or foraging, active hunting and bulldozing.

The feeding mode seen most often was that of browsing or foraging; this involved gathering and ingesting any edible materials that the cray discovered. Extensive field observations and feeding trials with captive *E. spinifer*, using a range of foods, have indicated that these animals will eat food particles of virtually any size from most types of substratum. Pieces may be bitten, scraped, or torn from larger pieces of flesh or plant debris using the mandibles, which are extremely powerful. Smaller particles may be sorted, selected and picked from the substratum using the chelae of the second or third pairs of pereopods and then passed to the mouth parts. Fine materials may be scraped directly from a surface by the mouth parts.

E. spinifer were occasionally observed to actively hunt and capture tadpoles at the study site. At such times, the actions of the crayfish were clearly predatory and capture of the tadpoles was not accidental. Movements of the cray were deliberate and slow, while the substratum was searched cautiously with the antennae. When a tadpole was encountered, the crayfish lunged forward assisted by a rapid extension of the abdomen, and the tadpole was captured using the great chelae. Captive *E. spinifer* were observed to show similar responses to small fishes, earthworms and smaller crays. In addition, wild *E. spinifer* have been observed on two occasions consuming small, live frogs.

The third type of behaviour may not be a feeding mode, but it is logical to report the observations at this point. This behaviour was observed in captive *E. spinifer*, housed in aquaria that had a bottom covered with sand from the study site containing small fragments of blackened, decomposing wood and charcoal. The sand had been sieved previously through 1mm mesh, in order to remove larger food particles that individuals could pick up using their chelae. After several days of starvation, these individuals began to 'bulldoze' the sand. This process involved the individual pressing its mouth and anterior cephalothorax onto the sand, and piling further sand against the anterior cephalothorax using the second and third pairs of pereopods. The crayfish then pushed the pile of sand forward with its mouth buried, propelled by the fourth and fifth pairs of pereopods, and holding the sand in place using the second and third pairs of pereopods and the great chelae.

Feeding Trials

In Trial 1 all foods were at first eagerly accepted by the experimental crays, but in all instances feeding activity declined over the first two months until individuals fed only occasionally, and generally showed little interest in food. During this trial five specimens died during or shortly after moulting; four did not moult, three moulted normally and ten moulted but failed to harden their new exoskeleton. Some individuals which moulted were an abnormal colour and all survivors were lethargic. The hepatopancreas in all survivors was extremely fragile and abnormally coloured when compared with wild stocks. Further analyses of relative hepatopancreatic weight were not considered meaningful and moult increments of experimental stocks were significantly less than increments of wild individuals with similar carapace lengths (Table 3).

TABLE 3

Comparison between the moult increments of wild stocks and experimental *E. spinifer* (Trial 1).

Experiment		Wild		Experiment		Wild	
C.L.*	I.*	C.L.	I.	C.L.	I.	C.L.	I.
61.8	4.7	61.7	4.9	49.4	2.6	49.1	5.0
44.6	2.8	44.4	5.2	49.1	1.3	49.3	4.9
78.2	2.7	74.3	2.6	47.5	3.1	48.6	5.2
53.7	5.9	54.0	5.1	63.7	3.7	64.0	7.9
51.5	5.2	51.4	5.7	73.8	2.9	77.9	5.0
71.5	4.2	73.0	3.9	67.5	3.9	67.1	6.1
60.4	3.9	61.3	7.1				

Paired t-test: $t = 3.76$; d.f. = 12; $p < 0.005$.

Mean difference Wild-Experiment = 1.7mm with 95% confidence limits of ± 1.0mm.

*Pre-moult carapace length (C.L.) and moult increment (I.) in mm.

Similarly in Trial 2, food was eagerly accepted initially but consumption then declined and became irregular. Although apparently in better condition than Trial 1 survivors, sample tests of these Trial 2 stocks indicated reduced levels of parameters measured. The mean hepatopancreatic fat content of individuals fed five days per week (0.054 g/g) was greater than the mean for those fed once a week (0.025 g/g), but wild *E. spinifer* had fat contents of 0.419–0.729 g/g. The level of feeding had no significant effect on protein concentration in gastric fluid of experimental crays, while differences between means for each feeding group, and between samples for each crayfish, were highly significant ($p < 0.005$, Table 4). Among wild *E. spinifer* gastric protein concentration showed considerable variability (Table 5). Again the moult increments of Trial 2 stocks were reduced in comparison with wild stocks.

DISCUSSION

Natural Diet, Feeding Behaviour

Formalin fixation prevented continuing trituration of ingested material by the gastric mill and preserved gut contents. The long intervals between initial and final samplings were planned so that any obvious dietary changes, either with season or more protracted periods, would be detected.

TABLE 4

Analysis of variation in the protein concentration in the gastric fluid of experimental *E. spinifer* (Trial 2).

Results for Individuals			
5 days/week feeding		1 day/week feeding	
Moult Stage	**Mean Protein Concentration***	**Moult Stage**	**Mean Protein Concentration***
Ce	166 ± 14	D1	33 ± 14
Ce	110 ± 14	De	204 ± 14
De	52 ± 14	De	48 ± 14
De	77 ± 14	De	371 ± 14
De	102 ± 14	De	73 ± 14
Mean	101 ± 109	Mean	145 ± 109

Analysis of Variance Summary				
Source of Variation	**d.f.**	**M.S.**	**F**	**p**
Feeding Level	1	39117	< 1	n.s.
Crayfish within Level	8	89152	267	< 0.005
Samples within Crayfish	10	335	8.1	< 0.005
Readings within Sample	60	41.3		

*Protein concentration expressed as mg/ml of crystalline bovine serum albumin, with 95% confidence limits based on the relevant Mean Square Errors from the Analysis of Variance.

TABLE 5

Analysis of variation in the protein concentration in the gastric fluid of wild *E. spinifer* (April 1978).

Mean Protein Concentrations for Individuals*	
Moult Stage Ce	**Moult Stage De**
93 ± 21	99 ± 21
49 ± 21	132 ± 21
141 ± 21	152 ± 21
160 ± 21	197 ± 21
81 ± 21	138 ± 21
Mean 105 ± 42	Mean 144 ± 42

Analysis of Variance Summary				
Source of Variation	**d.f.**	**M.S.**	**F**	**p**
Moult Stage	1	30968	2.33	0.25>p> 0.1
Crayfish within Stage	8	13318	19.7	< 0.005
Samples within Crayfish	10	678	18.3	< 0.005
Readings within Samples	60	37		

*Protein concentration expressed as mg/ml of crystalline bovine serum albumin, with 95% confidence limits based on the relevant Mean Square Errors from the Analysis of Variance.

The decision not to accurately quantify stomach contents, either in types of constituents or particle sizes, was made for the following reasons: lack of variation in stomach contents related to either sampling times or body size in *E. spinifer*, the nature of the stomach contents, the effect of the gastric mill in triturating and homogenising ingested material.

The stomach and hindgut contents of wild *E. spinifer* examined indicated that the natural diet consisted mainly of decomposing plant material, and that the larger food particles were almost exclusively woody plant tissues of terrestrial origin. Although *Triglochin procera* was abundant at several sites where specimens were collected, there was no evidence that this aquatic macrophyte was used as a food source, except occasionally when in a decomposed state. This concurred with aquarium observations that *E. spinifer* only consumed living plant material *(Egeria densa*, or filamentous green algae) after being starved for several weeks; then only a small quantity was consumed by a few individuals.

In contrast, both astacids and cambarids from European and North American freshwaters, have been found to consume large quantities of living macrophytes and algae, in addition to decomposing material (Hogger 1988). Locally, three Western Australian *Cherax* species have been reported as very destructive to macrophytes (Shipway 1951). The diet of *E. spinifer* is unusual in that only decomposing plant material is used.

The presence of fragments of woody plant tissue among smaller particles in the stomach, when the function of the gastric mill is considered, indicates that at least a portion of the finer material resulted from mechanical breakdown of larger particles similar to those identified. The gastric mill of *E. spinifer* is large and robust and well-suited for this purpose, but it is also possible that much of the finer material may have been ingested as fine, particulate detritus.

Although not done with the same degree of resolution the gut content analyses of *E. spinifer* yielded similar results to those from recently completed analyses for the Western Australian marron (*Cherax tenuimanus*) by O'Brien (1995). Given the low nutritional value of wood and studies of other species indicating relatively low utilisation of cellulose and fibrous carbohydrates (Lochmann et al. 1995), it is suggested that *E. spinifer* derives most nutrients from fine particulate organic matter associated with detritus. This fraction (particle size <40 μm) would include bacteria, microalgae, protozoans and fungi. The diet is known to be supplemented by predation and in Loddon River populations, which Turvey and Merrick (1997b) report have surplus males, cannibalism could be expected to be significant (Goddard 1988).

The attracting power of fish and meat baits as well as the hunting behaviour indicates that *E. spinifer* is not wholly detritivorous, it may also act as a scavenger or predator. Although, on present evidence, the bulldozing cannot be definitely described as feeding there are several observations indicating an association between available food and this behaviour pattern. In all cases bulldozing was preceded by a period of starvation and after individuals had made numerous, unsuccessful attempts to pick up food particles using the chelae. Immediately after bulldozing individuals release faeces consisting of fine black material. It is therefore suggested that very small particles of wood or charcoal are removed from the sand substrate during bulldozing.

If *E. spinifer* feeds preferentially on larger particles that can be easily manipulated by the chelae then preferred foods may have been in short supply in the Loddon. This suggestion is supported by the absence of obvious macroscopic plant debris in many parts of the stream and the presence of small sand grains among the stomach contents. Pond trials with another local omnivorous parastacid have indicated that good growth and survivorship are only achieved when benthic organic matter exceeds 0.5 kg/m^2 (Chavez and Mitchell 1995). But regardless of specific sources, it is clear that *E. spinifer* contributes significantly to the breakdown of terrestrial plant debris entering the stream. This allochthonous material is the basis of the energy budget in many aquatic systems (Bunn 1986).

Measurements of particle size of hindgut contents indicated that most ingested material was reduced by the gastric mill to a fine sludge. Indeed size ranges of particles measured, both in the stomach and hindgut of *E. spinifer,* were similar to those found in *Cherax tenuimanus* (O'Brien 1995). *E. spinifer* would thus have made incoming plant debris available to smaller detritivores, and greatly increased the surface area for microbial action.

In summary, *E. spinifer* must be considered an opportunistic feeder in the broadest sense, although its normal feeding role at the study site was that of detritivore; this finding is consistent with studies on other parastacids. There was no evidence of juveniles taking a higher percentage of aquatic invertebrates; a difference in diet between juveniles and adults has been suggested as a form of resource partitioning, to decrease competition for limited supplies (O'Brien 1995).

Feeding Trials

The two feeding trials were designed to investigate effects of differing food consumption on levels of gastric fluid protein and condition of the hepatopancreas, related to sex and size, but results were very limited.

The survivors at the end of Trial 1 were obviously in poor condition so no attempt was made to estimate hepatopancreatic fat content or protein concentration in the gastric fluid. The state of the hepatopancreas, inability to re-build exoskeletons and decline in feeding activity, suggest that this stress may have had a nutritional basis. Although Trial 2 stocks remained in outwardly normal condition, hepatopancreatic fat contents were a fraction of those measured in wild samples. Gastric fluid protein levels were highly variable, just as they were in wild specimens and moult increments were reduced. So it has not been possible to establish a relationship between feeding level and either hepatopancreatic fat or gastric protein concentration.

Comparisons and Recommendations

Other studies have shown that a number of decapods appear to use hepatopancreatic lipid as a nutrient reserve and both the dry weight and fat content values obtained for wild *E. spinifer* are similar to those previously reported for other crayfishes. There was considerable variation in the protein concentration of gastric fluid and hepatopancreatic fat content among wild *E. spinifer*, independent of moult stage. This suggests considerable variation in the feeding success of wild *E. spinifer* and food availability is widely recognised as a crucial factor controlling the abundance of crayfish populations (Flint and Goldman 1977; Hogger 1988; Lowery 1988). The difference in fat content of hepatopancreases of wild *E. spinifer* captured in August and January may indicate seasonal variations in feeding success, corresponding to observed seasonal variation in the average size of moult increments of individuals in different locations (Turvey 1980).

Future trials to elucidate relationships between feeding success and either hepatopancreatic fat content or gastric fluid protein concentration, should also take into account the possibility of seasonal changes in lipid or protein content of crayfish tissues, recently documented by Fernandes et al. (1995), as well as the activity of gut bacteria which have been demonstrated to produce a range of amino acids (Syvokiené and Mickéniené 1993). Suggested design features would include: utilisation of much larger experimental samples; commencement with all stocks at the same moult stage, with values from individuals moulting during the trial omitted from final analyses; and short duration, with trial completed before any substantial decrease in feeding activity. It is also suggested that whole fresh hepatopancreatic lobes be used for fat estimations and larger samples of gastric fluid would increase accuracy of protein analyses.

The response of *E. spinifer* to captivity needs further investigation. In contrast to

the experiments described above, juveniles maintained for growth studies appeared to grow normally over 12 months successfully undergoing several moults. Conditions under which these stocks were maintained differed from those in the feeding trials in two respects. The juveniles were only disturbed a few times during the year, and an actively decomposing bed of detritus was maintained in the tank. The success of this rearing system may indicate that *E. spinifer* is metabolically sensitive to repeated disturbance, or that some component of a complex, intact detrital system is necessary for adequate maintenance of physiological condition.

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